THE ANCYLOPODA, CHALICOTHERIUM AND ARTIONYX.[1]

By Henry Fairfield Osborn.

Chalicotherium was the most unique mammal of the Miocene period. So far as known at present, it combined cheek teeth of a distinctively ungulate type, ankle and wrist joints resembling those of the Perissodactyla, with highly modified phalanges, terminating in large cleft ungues which were undoubtedly covered with strong pointed claws. It was widely distributed over Europe, Asia and North America from the oligocene Phosphorites of France (*C. modicum*) to the early Pliocene of the Siwalik Hills (*C. sivalense*).

The recent discoveries of Filhol and Depéret in France have fully revealed the structure of the skull and limbs, but with the exception of the axis, little or nothing is known of either the vertebræ or scapular and pelvic arches. As we learn from these authors the *Chalicotherium magnum* of Sansan (Middle Miocene) was an animal taller than the grizzly bear. The head was about nineteen inches long and raised five feet above the ground. The limbs were rather slender, and a striking peculiarity of this species is that the fore limb is nearly twice as long as the hind limb (as indicated by the proportions of the radius and tibia). This was not the case in its upper Miocene ally (*Ancyllotherium pentelici*) from Pikermi, in which the limbs were heavy and of the same length. There were three toes upon each foot, but in both manus and pes, the fourth or outer digit was the largest instead of the third or middle digit as in the Perissodactyla. M. Filhol has represented *C. magnum* as fully plantigrade, but this appears to me an error; the perissodactyl displacement of the carpals and

[1] Under the title "The Affinities of *Chalicotherium*," this article was written some months ago. While it was in press, *Artionyx*, a new type of the order was discovered, and at the editor's suggestion, the article was held back to include a description of it.

tarsals, the structure of the ankle and wrist joints, and the terminal facets of the metapodials all indicate that the feet were sub-digitigrade. Displacement is very rare in plantigrade types. The proximal phalanges are peculiar in having the metapodial facets directed obliquely upward; both these and the median phalanges are short; the distal phalanges are very peculiar, they present a deep terminal cleft and were evidently drawn up or retracted, as in the cats, instead of being drawn down or flexed, as in the Edentates. Thus, it is probable that *Chalicotherium* walked more like a clumsy-footed cat than like the bear. The soles of the feet were slightly turned inward and the fore-limb was adapted to digging or partial prehension.

Restoration. The axial skeleton in the accompanying drawing is mainly based upon Filhol's restoration, but the scapula and pelvis are independently restored upon the perissodactyl model; the sloping trunk leads us to expect a rather broad pelvic basin. All the above parts are purely conjectural.

The proportions of the fore and hind limbs with each other and with the skull are based upon the figures of Depéret. In Filhol's drawing the skull is proportionately too small. The side views of the feet are after Filhol's excellent drawings, but the articular positions are drawn differently, for M. Filhol makes the animal fully plantigrade, while the metapodial and phalangeal and higher articulations prove that it was digitigrade.

What is the explanation of this remarkable assemblage of characters? Where shall we place Chalicotherium, with reference to the two great orders between which it seems to stand midway. If, observing the teeth and the carpus and tarsus, we relate it to Perissodactyla, we find ourselves placing a clawed type among hoofed types. Or is it to be considered an Edentate because of its claws and edentulous premaxillaries as Filhol has suggested? Or is it representative of a distinct order midway between the Ungulata and Unguiculata? It is too early to attempt a final solution of these questions. We must wait for the discovery of the middle and upper Eocene Chalicotheriidæ. It is evident from Gaudry's discovery of the

feet in the Phosphorites, *C.* (Schizotherium) *priscum*, that the finding of other Eocene types is not far off. In the meantime I have tentatively offered the suggestion that *Chalicotherium* is

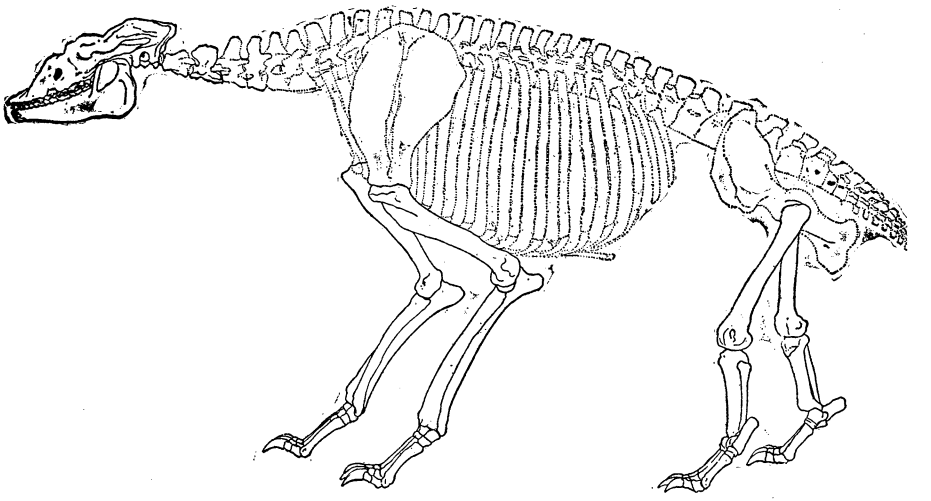


Fig. 1. Restoration of *Chalicotherium*. Modified from Filhol and Depéret.

distantly related to *Meniscotherium* of the lower Eocene (Wasatch), and that this may give us a clue to its zoological position. I will now expand and discuss this idea which may be expressed as follows:

That the group to which Chalicotherium belongs was derived from the Condylarthra of the lowest Eocene, with affinities to the Meniscotheriidae and primitive Perissodactyla. It represents a distinct order, the Ancylopoda (Cope). The likeness to the Unguiculates and especially to the Edentata is due to secondary adaptations and contains no proof of real affinity.

The *history of the discovery* of this animal is as unique as its structure, and illustrates the uncertain path of the vertebrate paleontologist. We are indebted for a full résumé, to Dr. Ch. Depéret, who has fully discussed the bibliography, structure and relations of this genus in his admirable memoir. Until

recently the skull and limb bones, wherever found, were placed not only in different genera but in distinct orders. The first remains discovered were the terminal phalanges, found in the upper Miocene of Eppelsheim in 1825; they were sent to Cuvier, who, noting the deep terminal cleft, named them *Pangolin gigantesque.* In 1833 Kaup found in the same beds the isolated upper molars which he naturally attributed to an ungulate, and named *Chalicotherium goldfussi* (syn. *antiquum*). Thus early began the confusion due to the wholly diverse affinities suggested by the phalanges and the teeth. In 1837 Lartet found the feet (in somewhat earlier Miocene beds of Sansan) which he supposed belonged to a huge edentate and termed *Macrotherium giganteum.* In 1853 Lartet also discovered a skull and teeth at Sansan; he was unaware of Kaup's priority and first called the skull *Anoplotherium,* but later separated it as *Anisodon*; Gervais, later, pointed out the priority of Kaup's term. In the upper Miocene of Pikermi Gaudry found feet and limbs quite different from the *Macrotherium* type; these he termed *Ancylotherium.* From the Phosphorites, in 1875, he described the teeth of a new species, *C. modicum,* and the feet of a supposed new genus, *Schizotherium priscum.* The skull and teeth were also found by Falconer in the Siwaliks of India and termed *C. sivalense.*

Considering this exceptional mingling in so many horizons, of one genus represented exclusively by skulls or teeth and another by feet and limbs, Filhol, in 1888, first advanced the conjecture that the two might really be one, and was happily able to confirm this by his own discoveries in Sansan. Forsyth Major independently arrived at the same conclusion from his explorations in the Pikermi beds. Finally, in his memoir, Depéret describes parts of a skeleton and skull found together at Grive St. Alban, in beds nearly contemporaneous with Sansan. In the meantime it is probable that a similar confusion has arisen with us. In 1877 Marsh announced the discovery of phalanges of a large edentate in the middle and upper Miocene of Oregon and Nebraska, and compared them with those of *Ancylotherium* rather than with any true edentates; he distinguished them by the coalescence of the first and sec-

ond phalanges as *Moropus* (species *distans, senex* and *elatus*). The first undoubted remains of *Chalicotherium* in this country were found by Garman in the Loup Fork (upper Miocene) and described by Scott and Osborn. Cope has also described a lower Miocene species (*C. bilobatum*) from the White River beds (Swift Current Creek) of Canada. It is not improbable that *Moropus* belongs to the same types.

Nomenclature and Synonomy. Depéret advocates an important modification in our nomenclature. He believes that the Eppelsheim type, to which the name *Chalicotherium* was originally applied, can be identified by the form of its phalanges with the Pikermi type (*Ancylotherium* Gaudry), and is, therefore, distinct from the Sansan type. For the latter he proposes to retain the name *Macrotherium* Lartet. If this proves to be correct these types should be distinguished as follows:

Middle and Lower Miocene. (Sansan, Grive St. Alban, ? Phosphorites.)	Upper Miocene, Lower Pliocene. (Eppelsheim, Pikermi.)
Macrotherium.	*Chalicotherium.*
Syn.: Anisodon, ? Schizotherium, ? Moropus.	Syn.: Ancylotherium.
Semi-arboreal and fossorial. Light skeleton. Fore-limb greatly elongated. Radius (= .70), tibia (= .29). Radius with large external, and small internal, fossa for humerus. Ulna distinct or very slightly coalesced with radius distally.	Quadrupedal. Heavy skeleton. Fore- and hind-limbs nearly equal. Radius and tibia of nearly same size; of heavy proportions. Radius with subequal external and internal fossæ of humerus. Ulna coalesced with radius.

While many striking differences separated these two types, especially in the proportions of the limbs, the teeth were substantially similar. A strong family relationship is also exhibited in a peculiarity of the feet pointed out by Gaudry, namely, the *proximal* phalanges were retracted and not the distal, while in the cats the *distal* phalanges are retracted and in the edentates the phalanges are not retracted at all but are flexed. In the edentates the foot is thrown upon its outer side; in the Chalicotheriidæ this was only partly the case.

Ungulate affinities of Chalicotherium. M. Filhol's view is that this genus belongs to a group which bridges the gap between the Edentates and Ungulates. When he showed me his newly discovered skeleton in 1889, I was especially struck by the perissodactyl character of the carpus and tarsus, and considered it best to leave the genus in the Perissodactyla as "an aberrant form, with nearest affinities to *Palaeosyops* and genera of that line." It has also been doubtfully placed near the Perissodactyla by Flower and Lydekker.

Depéret has now advanced sufficient evidence to exclude the edentate idea entirely and shows clearly that the resemblances which *Chalicotherium* bears to the sloths are purely superficial. As shown above the adaptations of the phalanges for prehension or digging involve an entirely different set of muscles from those employed in either the Cats or the Edentates. This genus has attained a somewhat similar functional result by a different route—a case of analogy but not of homology. So with the elongation and curvature of the fore-arm, the ultimate coalescence of the ulna and the radius, the backward direction of the olecranon, the cleft ungual phalanges. All these are independent and "parallel" or "homoplastic" adaptations. *Chalicotherium* is still more positively separated from the Edentates by the numerous ungulate characters which it displays.

Depéret is very much impressed by these ungulate structures and places this genus definitely among the Perissodactyla. Let us, therefore, examine the ungulate hypothesis. Upon the affirmative side is the structure of the molar teeth; they certainly bear a distant resemblance to those of *Anoplotherium* and a more striking likeness to those of *Palæosyops* and *Titanotherium*. The reduction of the upper cutting teeth may be regarded as a secondary adaptation which does not affect the question of ungulate affinity either way. There are really several questions involved; shall we waive the structure of the terminal phalanges and call this genus an Ungulate? Shall we then direct our attention upon the teeth and carpals and tarsals and call it a Perissodactyl, or shall we follow Cope and remove it entirely to the Unguiculata? Let us sum up some of its leading characters:

CHARACTERS OF CHALICOTHERIUM.

Shared by Ungulates.	*Shared by Perissodactyla.*	*Not found in Perissodactyla.*
Radius transverse proximally, with two fossæ for humerus.	Tridactyl manus and pes.	Not mesaxonic.
Tibia with two fossæ, spine and crest.	Astragalus and all carpal and tarsal facets diplarthrous.	Main axis through fourth digit.
Calcaneum with broad sustentaculum.		Secondary unquiculate modifications of limbs and phalanges.
Diplarthry in carpus and tarsus.		Third trochanter absent.
Jaws with elevated condyle and broad angle.	Buno-selenodont molar type.	Large curved tympanic bullæ.
Molar teeth of sexitubercular origin.		Reduction of upper incisors.

This table shows that there are many characters, beside the form of the phalanges, which excludes this family from the Perissodactyla proper. The detailed comparisons of the skull which Depéret institutes with *Palæotherium* and *Palæosyops* relate to structures which are shared by all primitive Ungulates. The only structures in which there is apparently conclusive evidence of a remote relationship to this great division of the Ungulates is first in the teeth and second in the carpus and tarsus. It remains, therefore, to be seen whether these also are products of homoplasy or "parallel adaptation," or whether they really evince affinity.

Now let us turn to the broader question. Is *Chalicotherium* to be classed as an ungulate or as an unguiculate in the Linnæan sense? We should, of course, compare it first with the primitive ungulata which exhibit many unguiculate characters. We are again guided partly by the excellent figures and descriptions given by Depéret of *C. magnum* (race Rhodanicum). The skull resembles that of the Ungulata Condylarthra in many features. The occiput is very low and broad and widely overhangs the condyles. There is a well arched sagittal crest and a rather small cranium. The lower jaw has an elevated condyle and a deeply extended angle. The external auditory meatus is widely open below and there is a large mastoid pro-

cess. The maxillary bones are high. All these characters are very similar to those in the skulls of the primitive Condylarthra, such as *Periptychus, Phenacodus* and *Meniscotherium.* We should also mention many cranial features which we believe belong to the category of secondary adaptive modifications; among such are the following: (1) the large curved cylindrical tympanic bullæ, (2) the feeble character of the nasals, premaxillaries and anterior portion of the mandibular rami. The latter modifications are associated with the reduction of the cutting teeth. Filhol has shown that the young individuals of Sansan have a full set of incisors, while in the adult the upper incisors are rudimentary or wanting.

There are other secondary features of note. The condylar facets are prolonged forward upon the basi-occipitals. The posterior face of the centrum of the axis is directed upward; this and the preceding features point to peculiar flexibility of the neck. The centrum of the axis is long and slender, the odontoid process is round, the spine is unusually long and high.

Looking again at the limbs we observe that the radius covers the entire front face of the ulna and presents two distinct fossæ for the condyles of the humerus. The tibia closely resembles that of some of the short-limbed ungulates in its cnemial crest and two fossæ for the femur, in its spine and distal grooves for the double trochlea of the astragalus which is like that in the short-footed *Aphelops.* This likeness to the ungulates, and especially to the perissodactyls, in the form of the upper foot bones and of their articulations with the metapodials is most striking. The calcaneum has a long tuber and very broad sustentaculum. The astragalus rests widely upon the cuboid, its tibial trochlea is very similar to that in the short-footed rhinoceroses. The cuboid, navicular and cuneiforms are, however, extremely flattened and specialized. The diplarthrous character of the carpus is precisely like that of Perissodactyla, the lunar rests upon the cuneiform and the scaphoid upon the magnum, while the metapodials abut laterally against the unciform and magnum.

Upon the whole we find that primitive and secondary ungulate characters decidedly predominate in the skull, teeth and skeleton. The secondary characters, especially in the ankle and wrist joints, are parallel with those in the perissodactyls, and are not mingled with unguiculate adaptations until we reach the phalanges.

Relation to the Unguiculata. Cope was the first to advocate the more radical view that this genus represents a distinct order. He wrote: "It has little relation to the family of Perissodactyla to which it has given the name (Palæosyops). Unlike the serial manus and pes of the edentata the carpus and tarsus are here diplarthrous in structure or displaced upon each other. While the Condylarthra are ungulate with an unguiculate carpus and tarsus, this order Ancylopoda presents the antithesis of including unguiculates with an ungulate carpus and tarsus." This antithesis he assigned as the main character of the new order.[2] He still considers the form of the terminal phalanges as of fundamental importance and believes (in a letter of May 14, 1892) that *Chalicotherium* must have been derived from some primitive unguiculate.

The ancestry of Chalicotherium. Without any knowledge of the ancestors of *Chalicotherium* we thus reach a dead lock. Shall the unguiculate structure of the phalanges outweigh the ungulate structures in other parts of the skeleton? Is it possible to derive such a skull and skeleton from any unguiculate or such terminal phalanges from any ungulate? In looking about for relatives of this genus we must now entirely discard the Palæosyops group, and hunt among the lowest Eocene types. The lowest Eocene unguiculates are wholly dissimilar. The only form at all similar is the genus Meniscotherium. Meniscotherium was a little plantigrade slightly larger than Hyrax, and of very similar proportions. It is found in the beds between the Wahsatch and Puerco and was even older than Coryphodon. The teeth are of the ungulate type known as

[2]Gill's term "Chalicotheroidea" was applied to these forms, considered as a super-family, equivalent to the Camelidæ, Giraffidæ, etc., and not as a suborder. Arr. Fam. of Mamm., 1872, p. 71–77.

"buno-selenodont." The feet are in the border region between the unguiculates and ungulates. This genus also occupies an isolated position; although placed by Cope in the family Meniscotheriidæ among the Condylarthra it is not even remotely related to any of the contemporary ungulates. Its molar evolution was precocious in both jaws, far more so than in Phenacodus. I was led to the idea that this might possibly be the long sought ancestor of Chalicotherium by the structure of the molar teeth. In 1886 Wortman regarded Meniscotherium as an ancestor of the Hyracoidea. Later Schlosser recognized the striking likeness of its molars to those of Chalicotherium, and considered it with Macrauchenia as a representative of Perissodactyla which had retained a primitive foot structure.

The comparison of the entire dentition of Meniscotherium and Chalicotherium led me in 1891 to the discovery of many very significant details of resemblance. In both, the anterior portion (or cutting teeth) of the dental series is reduced and the posterior or cheek teeth are enlarged. In both, the true molars have identically the same pattern in detail in both jaws, including the absence of the third lobe upon the last lower molar, which separates Meniscotherium from all early Condylarthra and Perissodactyla. I was especially struck also by the presence of a short posterior crest formed of the hypocone and hypoconule in the upper molars, and by the reduplication of the antero-internal tubercle (metaconid) in the lower molars. At the time only the upper tarsals of Meniscotherium were known; these possess the unguiculate characters which are exhibited in Phenacodus and all early ungulates but are distinguished by a *fibular facet* upon the calcaneum. It appeared to me altogether probable that the Wahsatch form was related to the ancestors of Chalicotherium, and that the question would be decided by the discovery of its feet. This discovery was reported sooner than was expected in Marsh's recent paper upon *M.* (Hyracops) *sociale* in which the fore and hind feet are fully figured.

The feet of Meniscotherium present only one feature which definitely points to those of Chalicotherium, namely, they are

functionally tridactyl, the outer toes being much shorter than the three median toes. Marsh describes the terminal phalanges as *intermediate* between hoofs and claws, the extremities are thin, slightly expanded, and apparently covered by thin nails. In other respects the feet are very primitive and exhibit all the unguiculate features we now invariably expect to find among the primitive ungulates, namely, (1) the "centrale" and possibly (2) the "tibiale," (3) the fibular facet upon

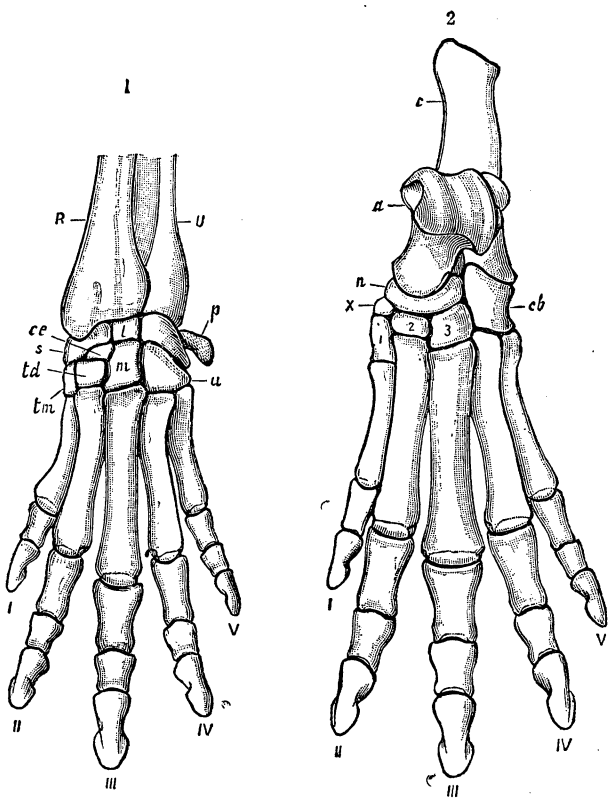


Fig 2. Fore and hind Feet of *Meniscotherium* (Hyracops) *sociale* after Marsh.

the calcaneum, (4) the "astragalar foramen," (5) the serial or undisplaced facets in both tarsus and carpus. As this was the parent ungulate type there is no insuperable difficulty in sup-

posing that the ungulate carpus and tarsus of Chalicotherium were derived from those of Meniscotherium.

The terminal phalanges present a greater obstacle; is it possible that having progressed only so far toward hoofs as to be called "intermediate," they have subsequently retrogressed into curved claw-bearing ungues? I consider this possible but not in itself probable. We must not forget the manus of the subungulate Lemurs which bears three or four terminal nails and one large claw; or the phalanges of the unguiculate Mesonyx which are cleft, but also flattened and very ungulate in appearance. The line of division between claws, nails and incipient hoofs was not very sharply drawn. Another difficulty is seen in the fact that the median toe (III) of Meniscotherium is enlarged, it is mesaxonic; while the lateral toe (IV) of Chalicotherium is enlarged.

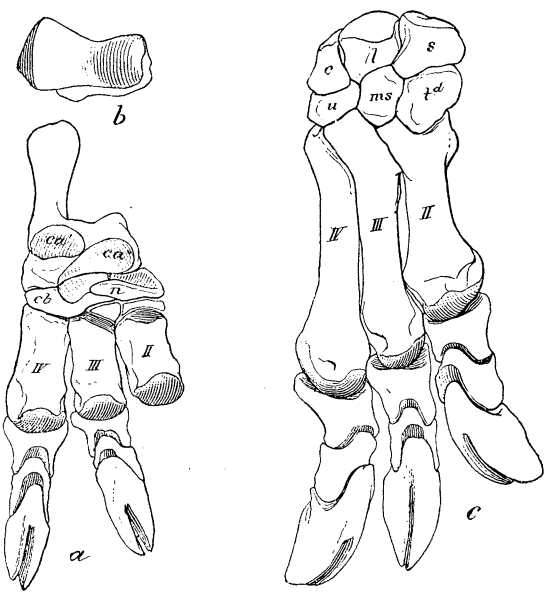


Fig 3. Fore and hind Feet of *Chalicotherium* after Gervais, (from Sansan.).

To offset these difficulties we find the striking similarities in the molar teeth already noted, and in the dental series as a whole. Meniscotherium is very exceptional in the absence of

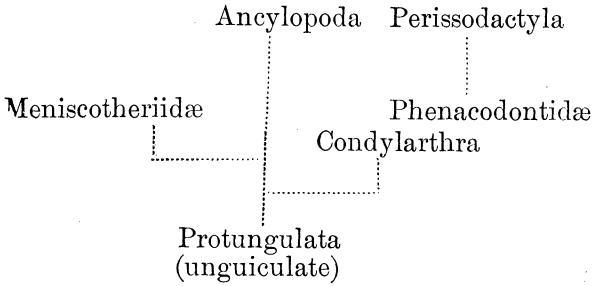
a third lobe to the last lower molar. The resemblance between the skulls of these two types is also very marked in the whole region behind the infra-orbital foramen. We see the same form of cranium, occiput, and auditory region.

I conclude, therefore, by giving a table of the resemblances and differences between the two types. Both are numerous. The question is, which are most fundamental?

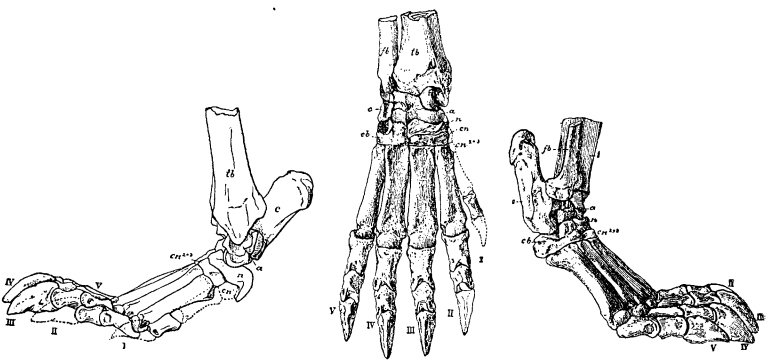
	MENISCOTHERIUM.	CHALICOTHERIUM.
1°	*Cutting teeth* somewhat reduced	Reduced or rudimentary.
	Upper molars, buno-selenodont	The same.
	A short posterior crest. Protoconule large.	The same. Protoconule reduced.
	Lower molars lopho-selenodont	The same.
	Metaconulid reduplicate. No 3rd lobe on M^3.	The same.
2°	Five *digits*. Functionally tridactyl. Mesaxonic.	Three digits. Structurally tridactyl. Not mesaxonic.
	Carpus and tarsus, serial, (unguiculate type)	Displaced (ungulate type).
3°	Centrale, tibiale, 3rd trochanter, entepicondylar foramen, Fibulo-calcaneal facet	All wanting.
4°	Terminal phalanges sub-ungulate.	Unguiculate.
5°	Plantigrade.	Sub-digitigrade.

Many of these differences are such as separate higher from lower forms, especially those under 3° and 5°. We witness the loss of the primitive characters under 3° in many distinct phyla, also the modification of the characters under 2° and 5°.

I have now endeavored to clearly state the pros and cons of this question. The evidence for the original ungulate affinities of the Ancylopoda seems to me much stronger than that for its purely unguiculate origin. Supporting this view is the strong likeness of the skull and teeth of Chalicotherium to those of Meniscotherium, and finally the analogies which it presents to the perissodactyls in the modernization of the feet, wrist and ankle. My conception of its origin and zoological relations can be expressed in the following diagram.



The purpose of this paper is not, however, to express a final opinion but to suggest inquiry. While agreeing with Cope that the Ancylopoda represent a distinct division of the mammalia, we must admit that the broad zoological relations of this division are yet to be determined.



a. Internal. *b*. Anterior. *c*. External.

Fig. 4. Right hind foot of *Artionyx gaudryi*.

Postscript.—The Discovery of Artionyx.

The hind foot of *Artionyx gaudryi* was found last summer by the American Museum party, under Dr. Wortman, in the White River Miocene of South Dakota.

The discovery of this foot was one of those complete surprises which render palæontological research so fascinating. As indicated in the above article, we were daily expecting to find remains of Chalicotherium in the lower Miocene of America, but no one could have anticipated finding a type related, and yet so entirely different.

As Chalicotherium may be broadly termed an unguiculate perissodactyl, so Artionyx may be called an unguiculate artiodactyl. This, in fact, sums up the main difference between these types when we add that the terminal phalanges in the former are cleft, and in the latter are uncleft.

If this foot of *Artionyx* had the metatarsals cut off half way down, no one would hesitate to call it truly artiodactyl. The tibia, fibula, astragalus and calcaneum, the navicular with its posterior hook for the great-flexor tendon, the conjoined ecto- and mesocuneiforms, the nearly even pairs of toes on either side of the middle line—all these structures bear a marked artiodactyl stamp. The entocuneiform is missing, but there is no doubt that it supported a first digit, of which the proximal phalanx is fortunately preserved.

The distal ends of the metatarsals and the phalanges exhibit the same sudden transition to an unguiculate type which we observe in *Chalicotherium*, in fact they bear a very marked resemblance to the corresponding parts in the feet of the carnivora, until we come to the terminal phalanges, which are short, deep and laterally compressed, but not hooked or retractile. As observed above, they are not cleft.

The foot differs as widely from that of Chalicotherium as that of the pig does from that of the tapir. It is somewhat hazardous to make a deduction from the foot alone, but we have ventured to divide the Ancylopoda into two subdivisions.

ORDER.	SUB-ORDERS.
Ancylopoda. Ungulate, with unguiculate terminal phalanges.	A. *Perissonychia* (odd clawed), with perissodactyl tarsus and mesaxial reduction. Ungues cleft.
	B. *Artionychia* (even clawed), with artiodactyl tarsus and paraxial reduction. Ungues uncleft.

Subsequent discoveries may show that these are merely two families—the Chalicotheridæ and Artionychidæ. This discovery rather strengthens the idea of the relationship of Meniscotherium to the Ancylopoda—for we observe in Artionyx the fibulo-calcaneal facet of the older genus, also the depression upon the inner side of the astragalus.

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